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Contributions of competition and climate on radial growth of *Pinus massoniana* in subtropics of China

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ABSTRACT

It is critical to investigate the effects of competition and climate on forest growth as they are main forces affecting forest dynamics. However, in subtropics of China such a study has never been conducted. Here we conducted a pioneer study to evaluate the effects of competition and climate on growth of Chinese red pine *(Pinus massoniana)* in mixed forests of subtropical China along a broad latitudinal gradient (23°N ~ 32°N). Twenty-three plots (20m × 20m) were randomly selected from 11 sites and competition and tree radial growth data were collected. Principal component analysis (PCA) was used to detect the potential spatial pattern in site-specific standard tree-ring chronologies during the common period (1990-2015). The linear mixed-effect models (LMMs) were employed to quantify the relationships between cumulated basal area increment (5, 10, 15, 20 and 25 years) of subject trees and six distance-independent competition indices. The relationships between tree radial growth and climate were evaluated by response analyses. Finally the best predicted competition index and climate factor were employed in a full model and their relative importance were calculated. The PCA results allowed classifying the mixed forests into southeastern and northern groups along the Nanling Mountains and Wuyi Mountains. LMMs results revealed that competition pressures mainly come from density and size of larger individuals. Response coefficients demonstrated that precipitation in September and sunshine duration in October influenced trees radial growth of southeastern group and northern group respectively. Our results clearly showed that effects of competition on tree radial growth decreased from southeast to north while effects of climates increasing over this large spatial scale. This is the first attempt to clarify the effects of competition, and further quantify the contributions of competition and climate on tree radial growth in China subtropics. Our finds will certainly contribute to a better policy-making for sustainable forest management.

1. Introduction

Forest ecosystem plays a vital role in terrestrial ecosystem, especially in carbon sequestration (Gardner et al., 2009; Pan et al., 2011). Studying the dynamic process of forest ecosystem within the context of global change is of great significances. Competition and climate are the main driving forces of forest dynamics and studying how they affect tree growth is the key to predict future forest dynamics (Casper et al., 2000; Jr and Mcnickle, 2011; Schoener, 1983; Tilman, 2004).

Both the effects of climate (Fritts, 2012; Grace et al., 2002; Lebourgeois et al., 2005) and competition (Casper et al., 2000; Fraver et al., 2014; Kozlowski, 1949) on trees growth have been widely studied. In addition, in the past decades some works explored the interaction between climate and competition. For example, Weber et al. (2008) found that drought was the cause of the different competitiveness of Scots pine (*P. sylvestris* L.) and pubescent oak (*Quercus pubescens* Willd.) in water limited inner-Alpine area. Ruiz-Benito et al. (2013) reported that in Spanish Forest, hot and dry exacerbated the death of

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trees at high competitive levels, especially for broadleaved species. Zhang et al. (2015) found that competition rather than climate was the primary factor causing boreal forest trees mortality and recruitment in western Canada. Sánchez-Salguero et al. (2015) revealed that competition rather than climate affected the tree growth of intensively managed scots pine (*P. sylvestris*) along an altitudinal gradient in central Spain. Young et al. (2017) studied the gridded data set from remotely sensed imagery of all forests in California and found that trees mortality disproportionately increased in dry and dense areas.

Although the interactive effects of competition and climate have been widely investigated, most studies were conducted at mid and high latitudes, and in the Mediterranean climate region at mid-latitudes, where temperature or water is the limiting factor of trees growth. In the subtropical monsoon region with sufficient rainfall and suitable temperature, relevant studies are rarely conducted (Rivas et al., 2005; von Oheimb et al., 2011).

The subtropical area of China, benefitting from uplift of Tibet Plateau, is far different from the same latitude area which is mostly arid (Yu et al., 2014). Subtropical China is covered by a large area of subtropical forests, which are shaped by East Asian Monsoon (Wu et al., 2007). The vegetation type in this region varies from broad-leaved evergreen forests to broad-leaved deciduous forests with increasing latitude (Teodoridis et al., 2011), in which a rich diversity of woody species are harbored (Su et al., 2015). In addition, the average net ecosystem productivity (NEP) of subtropical forest in China accounts for 8% of global NEP (Yu et al., 2014) with nearly 6% of global forest area (Keenan et al., 2015), indicating that forests in this region are a significant global carbon sink (Zhou et al., 2006). Therefore, how the forests respond to climate and competition is the key to studying the dynamics of forests in the subtropical China within the context of global change.

However in this critical region, only the effects of climate have been reported. For example Duan et al. (2012) studied a local scale tree ring width chronology in South China and found that winter temperature dominantly limited the radial growth of Chinese red pine (*P. massoniana*). Shi et al. (2015) reported that February to April precipitation had the most significant influence on the radial growth of *P. massoniana* in the east of subtropical China. Cai and Liu (2017) found that radial growth of Taiwan red pine (*P. taiwanensis*) in southeast China was limited by maximum temperature from previous March to previous October. How the competition influences trees radial growth in subtropical China is completely unknown, not to mention the comparing of the effects of competition and climate.

Herein, we conducted a large-spatial scale investigation of *P. massoniana* and aimed to reveal the potential impacts of tree-tree competition, and further compare the effects of competition and climate on radial growth. Dendrochronology, by coring tree stems, was used to measure the past radial growth (tree ring width, TRW; and basal area increments, BAI) of each tree. The specific objectives of this study were to 1) quantify the effects of competition and climate on the tree radial growth and; 2) determine the relative contributions of the competition and climate on growth of *P. massoniana* over this broad region and further clarify the mechanisms behind. We hypothesized that competition rather than climate is the major driver of tree radial growth, as the environment in subtropical China is suitable for trees growth and that the effects of competition and climate vary spatially over this large study region.

2. Material and methods

2.1. Study area and climatic data

The study sites are located at subtropical region of China (Fig. 1), with latitude ranging from 23 °N to 32 °N, and elevation ranging from 70 m to 1285 m (Table 1). This broad region is mainly affected by subtropical monsoon climate with hot and rainy summer and cool and dry winter. The most northern site Jigong (JG) Mountain located in central China is almost the northern boundary of subtropical region. The vegetation type is broad-leaved deciduous forests which are dominated by *P. massoniana,* Chinese sweet gum (*Liquidambar formosana* Hance), sawtooth oak (*Quercus acutissima* Carr.) and Chinese cork oak (*Quercus variabilis* Bl.). The most southern site Dinghu (DH) Mountain located in Guangdong province is the southern boundary of subtropical region of China. It is covered by broad-leaved evergreen forests which are dominated by *P. massoniana,* henry chestnut (*Castanea henryi* (Skan) Rehd. et Wils.), Chinese sweet gum (L. *formosana*), Schima (*Schima superba* Gardn. et Champ.) and swamp mahogany (*Eucalyptus robusta* Smith). Soil types are lateritic red earth soil and red earth, yellow earth and paddy soil from south to north.

Climatic data, including monthly precipitation, sunshine duration and maximum, mean, minimum temperature, of 121 meteorological stations in our study region were obtained from the National Meteorological Information Center of China Meteorological Administration (http://data.cma.cn). According to these data sets, the total mean annual precipitation sums during the period 1990–2015 is 1688 mm, while the annual cumulated sunshine duration is 1614.2 h. The mean annual maximum, mean and minimum temperatures are 23.2, 18.3 and 14.9 °C, respectively. Spatial annual climates were linearly interpolated based on the 121 meteorological records with a weight depending on the distance between interpolated point and the nearby meteorological station (Fig. 2). In general, the annual maximum, mean and minimum temperatures decreased from 27.6, 23.3 and 20.9 °C to 11.3, 9.1 and 6.0 °C with increasing latitude, annual precipitation decreased from 2145 mm to 795 mm, while the annual sunshine duration has no obvious spatial variance over the study region (Fig. 2).

2.2. Field and lab work

Competition in forest has been defined as negative effects of neighbors on a subject tree caused by sharing limited resources (e.g., nutrients, water and light) (Begon et al., 1996). According to the definition, four of the most important predictors for competition among individual trees were proposed: the density of competitors, the size of competitors, the distance between subject tree and competitors and the relative location of competitors (Pukkala, 1989a; Radtke et al., 2003). Until now more than 50 kinds of competition indices have been developed based on the above four aspects (Weigelt and Jolliffe, 2003). These indices, however, could be classified into two groups: distance-independent and distance-dependent indices. Distance-independent indices are developed in a given area or plot (Pukkala, 1989b), simply considering tree size, density of stems and area size (Filipescu and Comeau, 2007b; Rivas et al., 2005; Schröder and Gadow, 1999). Distance-dependent indices incorporate the relative location of neighbors on a subject tree (e.g., distance between the subject tree and neighbors, their influence-zones) (Larocque, 2002; Pukkala and Kolström, 1987; Rouvinen and Kuuluvainen, 1997).

Previous studies have compared distance-dependent and distance-independent competition indices and found that distance-independent indices are nearly as effective as distance-dependent indices in quantifying competition pressure (Canham et al., 2004; Filipescu and Comeau, 2007b; Stadt et al., 2007). Therefore, in this study field work was designed for obtaining the distance-independent competition data for its advantage of easier measuring. Field work was conducted in 2015 and 2016. Suitable sample sites were mainly selected in core areas of national nature reserves to make sure that tree growth was less disturbed by human activities. *P. massoniana* was chosen as subject trees because their tree rings are clear and easy for measuring and cross-dating (Xing et al., 2012). Based on the distributional area of *P. massoniana* in nature reserves, one to four plots (20 m × 20 m) were established in every site (Table 1). For each plot, firstly all of the trees were numbered and the species were identified, and then their

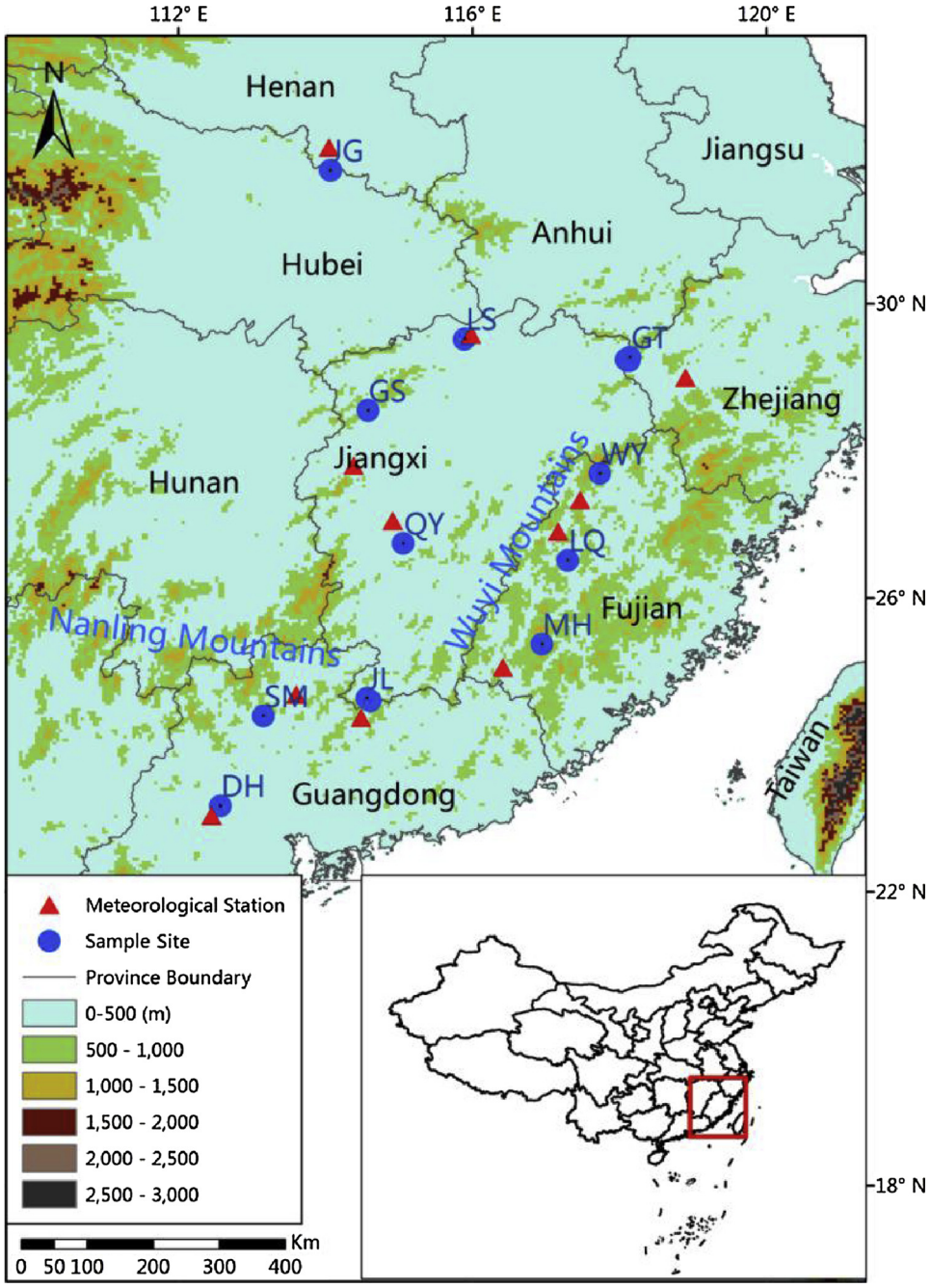

Fig. 1. Sample sites and the nearest meteorological stations.

diameters at breast height (DBH) were measured. Finally, total 23 sample plots in 11 sites were surveyed.

More than 20% of the total numbers of *P. massoniana* were randomly marked as subject trees in each plot to collect tree-ring cores. For every subject tree, two cores were drilled at breast height (1.3 m above ground) by an increment borer with 5.12 mm inner diameter, and bark thickness (BT) of each core was measured for further calculating the BAI. Competition radius was defined as 4 m based on the mean crown diameter of about 4 m (4.3 and 3.2 m in Dinghu Mountain and Jigong Mountain, respectively) of the dominant species we measured. The mean crown diameter of about 4 m of four pine tree species in a China national-wide survey was also reported (Zou et al., 2015). Then all individuals within 4-meter radius circle centered by every subject tree were recorded as competitors. Additionally cores from at least ten biggest *P. massoniana* individuals out of the plot were also drilled for help with cross-dating and developing site-specific chronologies.

In the laboratory, cores were firstly air-dried, then fixed in a wood groove with glue and tied with rope to prevent being out of shape. After the glue dried, samples were slightly sanded with progressively finer sandpapers to make the wood cells clearly visible under microscope. After visual cross-dating, tree-ring width of every sample was measured by Lintab system equipped with software TSAP-Win (Frank Rinntech, German). Quality of cross-dating was further checked by COFECHA (Holmes, 1983). Samples with poor quality (correlation coefficient between the sample and master series given by COFECHA was less than 0.32) or short length (less than 15 years old) were removed from the following analyses (< 8% of the total samples, number of finally used trees/cores shown in Tables 1 and 2).

Table 1
Sample plots information and characteristics.

Region	Lat.(N)	Lon.(E)	Elv.(m)	Trees (in plot)	No. of stems of *P. massoniana* / other species (ha^{-1})
DH1	23°09′48″	112°33′44″	70	7	600/1725
SM1	24°23′33″	113°09′23″	116	8	950/375
SM2	24°23′45″	113°09′10″	116	8	650/1350
SM3	24°23′45″	113°09′17″	126	12	1100/425
JL1	24°36′04″	114°36′42″	378	9	675/1550
JL2	24°38′09″	114°33′42″	356	8	500/1800
MH1	25°18′14″	116°52′20″	1285	7	775/3100
MH2	25°22′11″	116°56′36″	789	8	575/2100
LQ1	26°30′48″	117°17′47″	765	10	1250/1100
QY1	26°44′33″	115°3′31″	570	6	450/1250
QY2	26°44′36″	115°3′28″	120	10	1225/1450
WY1	27°41′45″	117°44′14″	464	9	425/3050
GS1	28°33′12″	114°34′43″	431	9	450/3550
GS2	28°33′25″	114°34′48″	534	7	225/3650
GS3	28°33′27″	114°34′50″	549	8	350/3475
GT1	29°13′49″	118°7′60″	410	14	750/4250
GT2	29°14′48″	118°5′28″	344	12	925/4875
GT3	29°14′50″	118°5′54″	471	7	250/5000
GT4	29°16′20″	118°8′17″	470	7	1050/3725
LS1	29°31′16″	115°53′27″	158	9	800/3075
LS2	29°31′57″	115°54′5″	186	8	1650/3675
JG1	31°49′12″	114°03′51″	180	5	825/2700
JG2	31°49′28″	114°04′28″	190	5	800/2225

2.3. Tree-ring data and competition indices

2.3.1. Development of site-specific chronologies and spatial classification

ARSTAN was employed to develop site-specific tree ring width chronologies for all cores from the same sample site (including cores from both inside and outside of all plots each site) (Cook, 1985). Smooth spline with 50% frequency cut-off was used to remove age-related grow trend, and the detrended series were averaged by bi-weighted robust mean method to develop the final chronologies. Common period analysis was done over the period 1990-2015. Expressed population signal (EPS), correlation between cores (Rbar), signal-noise ratio (SNR) and variance accounted for the first component (PC1) were calculated to evaluate qualities of these chronologies (Table 2). Given the wide latitudinal gradients with different environment conditions, principle component analysis (PCA) was employed to test the site-specific chronologies' homogeneity and to classify the sites into sub-regions.

2.3.2. Basal area increment (dependent variable)

Package "dplR" (Bunn, 2008) of R software (version 3.4.1) (R Core Team, 2015) was used in calculating BAI of subject trees. For every individual tree, the sum of BAI over different time intervals was calculated as the indicator of tree radial growth (5, 10, 15, 20 and 25 years from the outmost ring, here for 2015 or 2016, abbreviated to sum5, sum10, sum15, sum20 and sum25 hereafter). Some of the cores (˜11%) were not drilled to pith, so we calculated the BAI with the following equation, which may calculate the BAI without collecting the pith and had been mentioned in previous studies (Biondi, 1999; Biondi and Qeadan, 2008; Huang et al., 2013).

$$BAI_{it} = \pi\left(\frac{DBH_i}{2} - BT_i - \Delta R_{it}\right)\Delta R_{it} \quad (1)$$

where BAI_{it} (mm^2) indicates the basal area increment of the ith subject tree of year t; DBH_i (mm) and BT_i (mm) represent the measured DBH and bark thickness of the ith subject tree; ΔR_{it} (mm) is the tree-ring width of the ith subject tree of year t. Finally, the unit of BAI_{it} was converted to m^2.

2.3.3. Competition index (independent variables)

As we focused on competition effects on individual trees, the competition indices were calculated as tree level rather than stand level. Six distance-independent competition indices were calculated based on the field records, including density of competitors (N, stems/ha), sum of competitors' DBH (SDBH, m/ha), sum of competitors' stand basal area (SBA, m^2/ha), and these three indices that only consider the competitors thicker than each subject tree (NGR, SDBHGR and SBAGR). Competition indices were calculated as below (Huang et al., 2013):

$$CI = \frac{m}{A}\sum_{j=1}^{n_j}(DBH_j)^k \quad (2)$$

where CI is competition index; A (ha) is the competition area around subject trees, in this study it is a constant of 0.005; k is the adjustment for exponent ($k = 0$ for N, $k = 1$ for SDBH, $k = 2$ for SBA); m is the scaling factor, either m = 1 when $k = 0$ or 1, or $m = \pi/4$ when $k = 2$; n is the number of competitors; DBH_j (m) is the diameter at breast height of the competitor tree j. The competition indices were firstly calculated for both intra- and inter- species, and then all the competitors were mixed together to calculate the six competition indices again.

2.4. Modeling the growth-competition relationship

Pressure of competition varies with forest developing over time (Huang et al., 2013). Thus the ideal method to investigate competition on subject tree radial growth over time is to calculate the competition indices every year. However, it is impractical to obtain such competition level data due to time-consuming and laborious. In this case we assumed that the relative competition pressure of a subject tree from neighbor trees would be constant because of its growing size over time. Thus the competition indices calculated by current size of competitors can be used for simulating subject tree radial growth over different time intervals.

First the intra- and inter- species competition indices were assessed using linear-mixed model when considering species as dummy variable. However, the effects of intra- and inter- species competition on radial growth was not significant ($p > 0.01$). Finally the cumulated BAI of every individual during same time interval (dependent variable) was modeled as a function of one of the six competition indices (independent variable, all competitors without considering species) through linear mixed effects models (LMM). As the cumulated BAI series did not follow normal distribution, log function was employed to link the linear relationships. The competition indices were analyzed as fixed effects with random intercept for each plot. The model was presented as follows:

$$Log_{BAI} = a + b \times CI + \delta + \varepsilon \quad (3)$$

where CI is one of the competition indices; a and b are fixed effects; δ presents the random intercepts across plots; ε is the error of within plot measurements. LMMs were performed using R package "nlme" (Pinheiro et al., 2014). The model performance was evaluated by R package "MuMIn" (Barton, 2009), in which marginal R-square (variance explained by fixed factors) and conditional R-square (variance explained by both fixed and random factors) were calculated ((Nakagawa and Schielzeth, 2013; Johnson, 2014).

2.5. Computation of regional climate data

Based on the results of PCA, site-specific chronologies could be divided into two sub-regions (Fig. 3). The first principle component (PC1) of all site-specific chronologies in one sub-region was calculated as regional chronology. The regional monthly climate data were employed as first principal components (PC1) of all monthly meteorological data (e.g., sunshine duration, temperature and precipitation), which were recorded by meteorological stations closest to the sampling sites in the

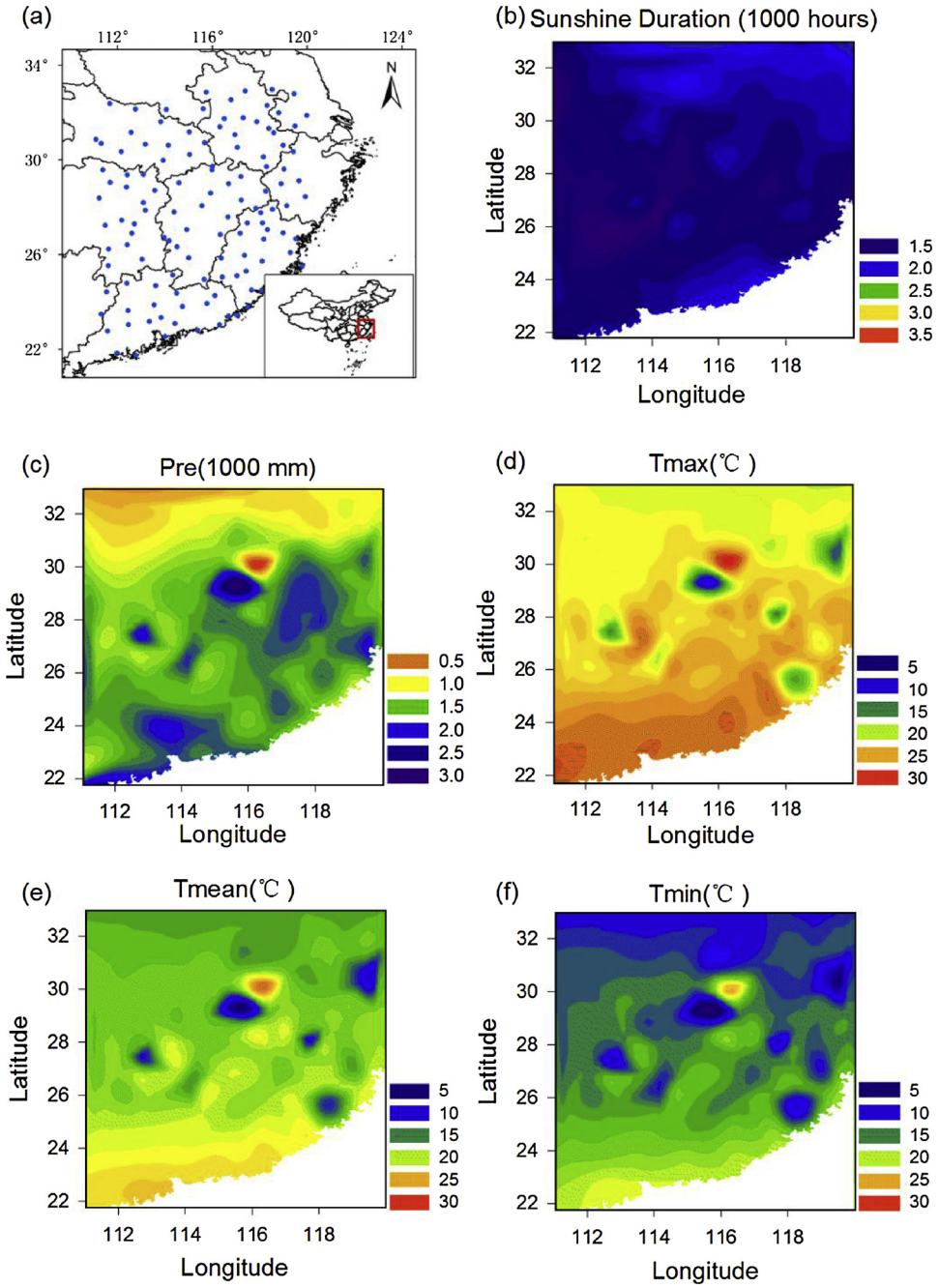

Fig. 2. The 121 metrological stations (a) records interpolated mean annual Sunshine duration (b), precipitation (c), maximum temperature (d), mean temperature (e) and minimum temperature (f) over a large spatial scale.

sub-region. Bootstrapped response analysis (1000 times) between the regional chronologies and regional climates (from previous September to current December) were conducted using R package "treeclim" (Zang and Biondi, 2015). As the BAI and tree-ring width were different indicators (biotic and abiotic indicators respectively, Biondi and Qeadan, 2008), developing of regional standard BAI chronologies followed by computation the relationships between them and regional monthly climates were assessed in the same method with tree-ring width to confirm the driven factors of climate to tree radial growth.

2.6. Relative contributions of competition and climate on trees radial growth

To disentangle the relative contributions of competition and climate on trees radial growth, the CI and climates should be used in one linear model. As these two independents are in temporal inconsistent, multi-year average of the most significant climate factors (the time interval depends on the results of 2.4 section) were also calculated. Then the best predicted CI and averaged climates were used in one linear model to fit the BAI. The model was presented as follow:

$$Log_{BAI} = a_0 + a_1X_1 + a_2X_2 + \varepsilon \quad (4)$$

where a_0, a_1 and a_2 are intercept and slopes; X_1 and X_2 are the best predicted CI and climate factor; ε is the error of within plot measurements. Then R package "relaimpo" was employed to calculate the relative contributions of competition and climate on tree radial growth (Grömping, 2006).

Table 2
Statistics of site-specific standard tree ring width chronologies and results of common period analysis over 1990–2015. Trees/Cores, number of all cross-dated trees and cores; Rbar, mean correlation coefficients between cores; EPS, expressed population signal; SNR, signal-noise ratio; PC1, variance accounted for the first principal component.

Site	Trees/Cores	Time span	Stand age	Rbar	EPS	SNR	PC1
DH	39/75	1956-2015	55 ± 3	0.238	0.890	8.099	0.311
SM	64/112	1974-2015	31 ± 6	0.216	0.882	7.440	0.289
JL	29/53	1949-2015	34 ± 13	0.272	0.829	4.863	0.331
MH	34/57	1986-2016	30 ± 1	0.212	0.861	6.174	0.266
LQ	18/27	1953-2015	49 ± 7	0.126	0.722	2.598	0.248
QY	31/53	1956-2015	33 ± 8	0.353	0.939	15.284	0.393
WY	18/31	1955-2015	59 ± 1	0.140	0.808	4.217	0.226
GS	57/105	1960-2016	50 ± 3	0.190	0.950	18.965	0.257
GT	64/121	1953-2015	41 ± 8	0.215	0.964	26.592	0.287
LS	37/63	1970-2016	35 ± 6	0.369	0.938	15.215	0.409
JG	32/55	1926-2015	59 ± 7	0.432	0.970	31.983	0.466

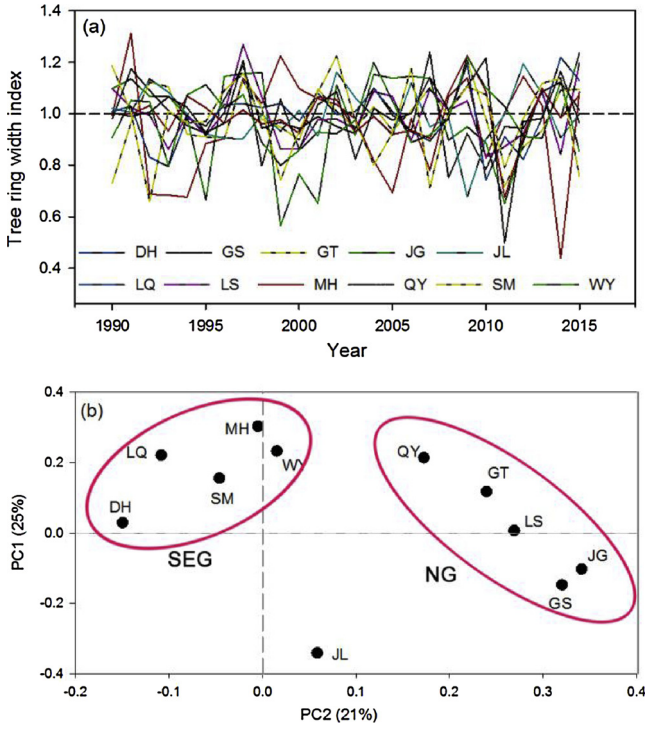

Fig. 3. Site-specific standard tree ring width chronologies during 1990–2015 (a) and their PCA results (b). The red circles indicated two obvious groups along the axis of PC2. The SEG and NG indicated the southeastern group and northern group, respectively (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

3. Results

3.1. Statistics of site-specific chronologies

Totally, 752 cores from 423 trees were analyzed, among which 195 trees are located inside of the plots (Tables 1 and 2). Chronologies are presented in Fig. 3a and statistical results are listed in Table 2. Though the EPS of chronologies from sites LQ, WY and JL are low (usually use 0.85 as the threshold, Wigley et al., 1984), the cores of these three sites were still used for modeling, as we mainly focus on the regional scale relationship between cumulated radial growth of individual trees and the competition pressure.

3.2. Spatial patterns in tree radial growth

The PCA results for site-specific chronologies show that the first two components explain 46% (25% for PC1 and 21% for PC2) of the total variance of chronologies. The ordination along the two axes (PC1 and PC2) in Fig. 3b present a clear separation of all the chronologies. DH, LQ, MH, SM and WY are a group located in southeastern of the study region (abbreviate to SEG); while GS, GT, JG, LS and QY are northern group (abbreviate to NG). Compared with their locations in Fig. 1, these two sub-regions are separated naturally by a topographic feature, Wuyi Mountains and Nanling Mountains (Fig. 1). Therein JL is in the transition section along PC2 axis, and its location is in Nanling Mountains, the boundary of these two sub-regions. Considering the location of JL is at low latitude, it was counted into SEG for modeling. Correlation coefficient between the two regional ring-width chronologies (PC1 of SEG and NG site-specific chronologies respectively, which explained 35% and 40% of the total variance) was 0.24 ($p > 0.05$). It shows that tree radial growths in these two groups have no significant relationships. Therefore, all the analyses are conducted for two sub-datasets (SEG and NG).

3.3. Statistics of competition indices

Following the spatial patterns of site-specific tree ring width chronologies, the statistics of competition indices were calculated separately for SEG and NG (Table 3). One-way ANOVA showed that there are significant differences in the competition pressure between the two groups (F values range from 5.8 to 12.4, $p < 0.05$). The mean stem density of SEG is higher than that of NG, while the mean tree size of SEG (mean DBH and stand BA) is smaller than that of NG. The minimum values of NGR, SDBHGR and SBAGR reach to 0, representing that the subject tree is thicker than all the competitors and indicating quite low competition pressure.

3.4. Relationships between cumulated BAI and competition

LMMs were conducted for the two groups SEG and NG separately (Tables 4 and 5). For SEG, the models computed for cumulated BAI over the past 15 and 20 years show the higher R^2 values than other time intervals. In the same time interval, the NGR, SDBHGR and SBAGR fitted integrated growth of subject trees have the highest R^2. The best model fits are found for BAI over the past 20 years, where higher conditional R^2 of 0.69 and 0.66 were found when NGR and SDBHGR are predictors respectively. For NG, the models for 15–25 years cumulated BAI perform better than other time intervals. Similar to SEG, the cumulated BAI of trees in NG are well fitted by NGR, SDBHGR and SBAGR. Among all indices, NGR and SDBHGR are the best predictors for the interval of 25-year integrated growth (conditional R^2 are 0.49 and 0.47 respectively). The best fitted models for both SEG and NG are

Table 3
Characteristics of the competition indices of the southeastern and northern groups.

`	N (stems/ha)			SDBH (m/ha)			SBA (m^2/ha)			NGR (stems/ha)			SDBHGR (m/ha)			SBAGR (m^2/ha)		
	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min
SEG	8000	2432	200	656	225.6	9.6	105.6	27.2	1.6	1000	184	0	235.2	44.8	0	72.8	9.6	0
NG	6600	3160	400	573.6	279.2	80.8	139.2	36.8	9.6	800	264	0	264.8	71.2	0	70.4	15.2	0

Table 4
Results of the linear mixed-effects models for the southeastern group (SEG).

Time interval	Competition indices	a	b	Marginal R^2	Conditional R^2
5	N	−0.16	−0.43	0.10	0.44
	SDBH	−0.05	−0.55	0.13	0.47
	SBA	−0.19	−0.39	0.07	0.52
	NGR	−0.18	−0.54	0.31	0.59
	SDBHGR	−0.20	−0.48	0.21	0.60
	SBAGR	−0.30	−0.35	0.11	0.58
10	N	−0.11	−0.37	0.10	0.40
	SDBH	−0.04	−0.44	0.11	0.41
	SBA	−0.15	−0.32	0.06	0.45
	NGR	−0.07	−0.55	0.42	0.60
	SDBHGR	−0.10	−0.48	0.29	0.59
	SBAGR	−0.20	−0.35	0.15	0.55
15	N	−0.07	−0.35	0.10	0.43
	SDBH	−0.03	−0.39	0.10	0.44
	SBA	−0.13	−0.28	0.05	0.47
	NGR	**−0.04**	**−0.52**	**0.45**	**0.67**
	SDBHGR	**−0.06**	**−0.46**	**0.32**	**0.65**
	SBAGR	−0.16	−0.34	0.17	0.60
20	N	−0.11	−0.31	0.08	0.44
	SDBH	−0.08	−0.33	0.08	0.44
	SBA	−0.16	−0.24	0.05	0.48
	NGR	**−0.05**	**−0.51**	**0.45**	**0.69**
	SDBHGR	**−0.08**	**−0.45**	**0.32**	**0.66**
	SBAGR	−0.17	−0.34	0.18	0.62
25	N	0.03	−0.45	0.15	0.37
	SDBH	0.02	−0.42	0.12	0.36
	SBA	−0.11	−0.27	0.07	0.35
	NGR	−0.00	−0.57	0.45	0.63
	SDBHGR	−0.06	−0.43	0.34	0.59
	SBAGR	−0.16	−0.31	0.21	0.53

Table 5
Results of the linear mixed-effects models for the northern group (NG).

Time interval	Competition indices	a	b	Marginal R^2	Conditional R^2
5	N	−0.44	−0.01	0	0.34
	SDBH	−0.30	−0.15	0	0.36
	SBA	−0.38	−0.08	0	0.34
	NGR	−0.11	−0.46	0.19	0.36
	SDBHGR	−0.15	−0.41	0.14	0.35
	SBAGR	−0.21	−0.32	0.09	0.34
10	N	−0.27	−0.10	0	0.35
	SDBH	−0.18	−0.18	0.01	0.36
	SBA	−0.30	−0.06	0	0.34
	NGR	−0.03	−0.45	0.24	0.39
	SDBHGR	−0.06	−0.40	0.18	0.36
	SBAGR	−0.14	−0.30	0.10	0.35
15	N	−0.18	−0.19	0.01	0.39
	SDBH	−0.14	−0.23	0.01	0.40
	SBA	−0.29	−0.07	0	0.37
	NGR	**−0.02**	**−0.45**	**0.27**	**0.42**
	SDBHGR	**−0.06**	**−0.40**	**0.19**	**0.40**
	SBAGR	−0.13	−0.30	0.11	0.38
20	N	−0.11	−0.27	0.02	0.43
	SDBH	−0.10	−0.27	0.02	0.44
	SBA	−0.29	−0.09	0	0.41
	NGR	**−0.05**	**−0.43**	**0.24**	**0.44**
	SDBHGR	**−0.08**	**−0.37**	**0.17**	**0.42**
	SBAGR	−0.15	−0.28	0.10	0.41
25	N	−0.13	−0.30	0.03	0.46
	SDBH	−0.16	−0.25	0.02	0.47
	SBA	−0.33	−0.07	0	0.45
	NGR	**−0.07**	**−0.44**	**0.26**	**0.49**
	SDBHGR	**−0.12**	**−0.37**	**0.17**	**0.47**
	SBAGR	−0.19	−0.27	0.09	0.46

selected, and their observations and fitted values are shown in Fig. 4.

3.5. Relationship between tree radial growth and climates

The variances explained by PC1 of monthly climate factors range from 0.73 to 0.93 for sunshine duration of SEG and 0.58–0.87 for sunshine duration of NG; for temperature the explained variances range from 0.69 to 0.97 and from 0.74 to 0.93 for SEG and NG; while 0.366–0.909 and 0.394–0.728 for precipitation of SEG and NG respectively. These high explained variances show the reliable of regional climates. The response analysis between these monthly regional climate factors and regional-scale chronologies indicate that the NG trees radial growth and sunshine duration in October of current year have a significant positive relationship ($r = 0.359$, $p < 0.05$), while precipitation in September significantly and negatively affect tree radial growth of SEG ($r = -0.405$, $p < 0.05$) (Fig. 5). In addition, even though the coefficient between regional chronology of SEG and temperature in September is high (0.445), it is not statistical significant based on bootstrapped results ($-0.046 < r < 0.762$). The regional standard BAI chronologies response to similar climate factors compared to the regional tree-ring width chronologies did (Appendix S1), which confirm that precipitation in September and sunshine duration in October are the major driven factors for tree radial growth in SEG and NG respectively.

3.6. Relative importance of competition and climates

Based on the results in 3.4 and 3.5 sections, NGR and 20-years averaged September precipitation were finally chosen as independent variables to fit the cumulated 20-year BAI of SEG ($R^2 = 0.55$). While for NG, the 25-year cumulated BAI was modeled by NGR and 25-year averaged October sunshine duration ($R^2 = 0.44$). The relative contributions of independent variables in these two models are showed in Fig. 6. From southeastern region to northern region, the relative contribution of competition decreases from 0.98 to 0.75, while the effect of climate increases from 0.02 to 0.25.

4. Discussion

Subtropical forest in eastern Asia is a crucial forest area for its functions of carbon dioxide uptake and biodiversity protection. Although tree-tree competition and climate are main drivers of forest growth and succession in this region, their effects and relative contributions on subtropical forest growth were still unclear. In this study, we investigated *P. massoniana* in subtropical regions of China and quantify the effects of distance-independent competition indices and climate on radial growth of trees. Results showed that tree radial growth spatially varied and is significantly affected by the density and size of thicker trees. And while the effects of climate increase from southeastern region to northern region, the influence of competition is diminishing. These findings well confirmed our hypotheses and will certainly help in developing more scientific afforestation and deforestation measures to achieve sustainable forest management in subtropics.

4.1. Spatial variation of tree growth and relative climate limitation

The two regions classified by PCA indicated different growing conditions for pine trees. Previous studies have found that the obstruction of East Asia Monsoon by Nanling Mountains and Wuyi Mountains lead to more annual precipitation in southeast than in north in subtropical China (Endo et al., 2005; Guo and Zhi, 2009; Zeng et al., 2010). The vegetation types vary from subtropical monsoon evergreen broad-leaved forest in the south to subtropical evergreen and deciduous broad-leaved mixed forest in the north (Wu, 1995). In addition, the soil type changes from lateritic red earth soil to red earth, yellow earth and

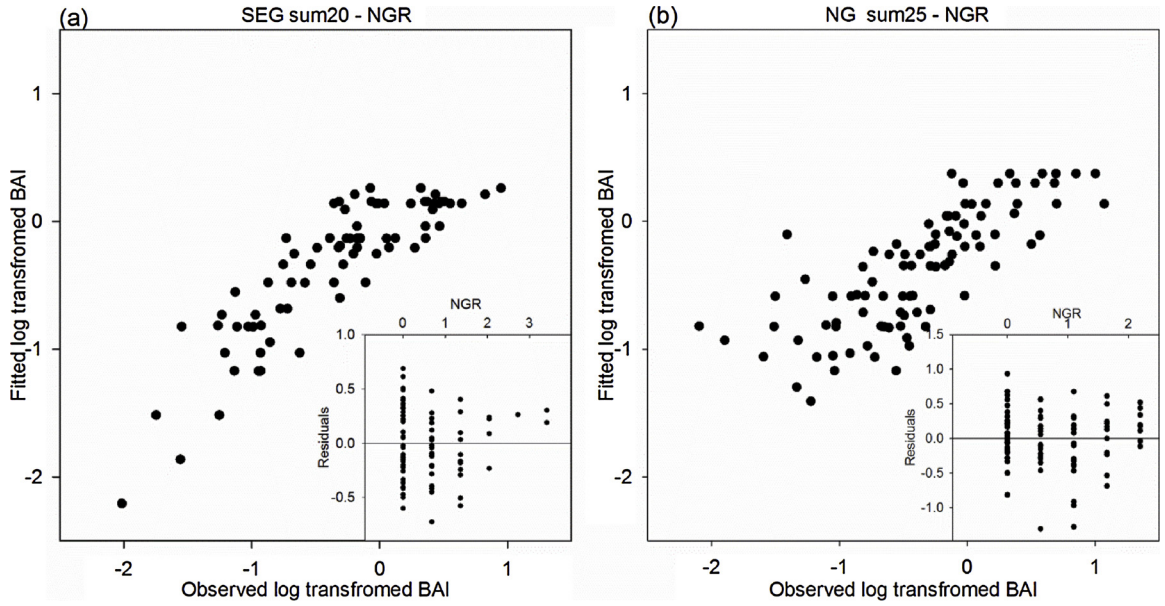

Fig. 4. Relationships between observed and best predicted BAI of southeastern group (SEG) and northern group (NG); Small panels show the distribution of residuals; NGR means the number of competitors which are thicker than the subject tree; sum20 and sum25 mean the cumulated BAI for 20 years and 25 years, respectively.

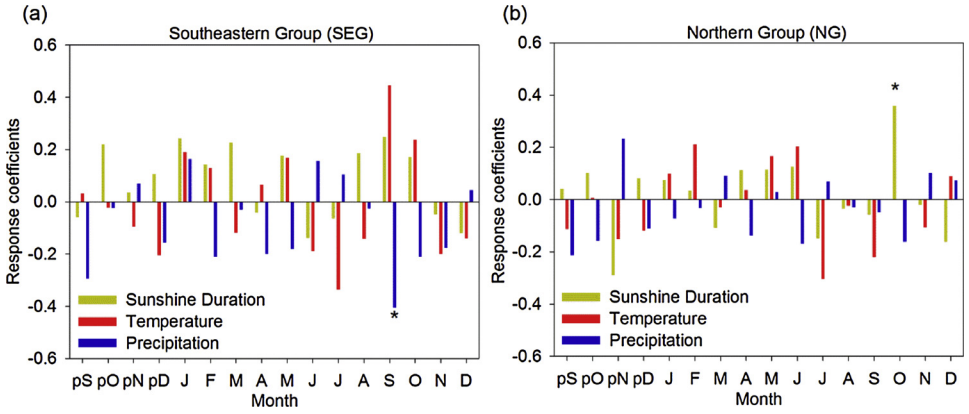

Fig. 5. Response coefficients between PC1 of site-specific standard tree ring width chronologies and PC1 of monthly climatic factors (sunshine duration, mean temperature and precipitation); * indicates the significant at level of 0.05.

paddy soil (Xi and Zhang, 1982). These spatial variations of abiotic factors and biotic factors such as the competition, forests communities and soil microbial species, would together lead to the differences in tree radial growth between SEG and NG.

In general the most common variances among tree-ring width chronologies are considered as climate signals (Fritts, 2012). The results of PCA for all the site specific tree-ring width chronologies showed that PC1 reflects the common signals in tree growth at SEG sites, and PC2 reflects the main signals of the NG sites. Therefore, the growth-climate response analysis between the two regional tree-ring width chronologies and regional monthly climates indicated that September precipitation is the main driver of PC1, and October sunshine duration is the main driver of PC2.

The autumn climatic factors (precipitation in September and sunshine duration in October) significantly influenced tree radial growth, which demonstrated that in subtropical regions, trees would still grow when environment conditions are favorable in autumn (Cai et al., 2017; Harley et al., 2012; Huang et al., 2018).

The precipitation in September has significant negative effects on tree radial growth in SEG. One explanation is that more rainy days in September would lead to shortage of photosynthesis and finally reduced the annual tree-ring width. Another explanation is that in rainy days, the vapor pressure deficit (VPD) decreases, which will lead to water demand reducing from the roots (Senock and Leuschner, 1999), resulting in a decrease of daily sap velocity and flow rate (Luo et al., 2016), which would reduce the canopy transpiration and exchange of CO_2 (mainly caused by closure of stomata) and finally slow down the photosynthesis rate (Granier, 1987; Jones, 1998). Huang et al. (2018) using the recently developed micro-sampling approach, have found that xylem growth of Chinese red pine in subtropical China peaked in the current autumn (September-November), with the highest rate of cell division when warm and dry climate is dominant, which further confirmed our results.

The significant positive effects of sunshine duration in October on tree radial growth in NG indicated that sunshine duration in October is the most important factor for tree radial growth in NG. Longer sunshine duration in October would increase photosynthetic rate (Aerts, 1999; Hafner et al., 2014). In addition, sunny days are commonly coupled with warm temperature, which could prolong the growing season (Fritts, 2012) and finally increases the tree-ring width.

4.2. Tree-tree competition

The linear mixed effects models were well fitted for tree radial

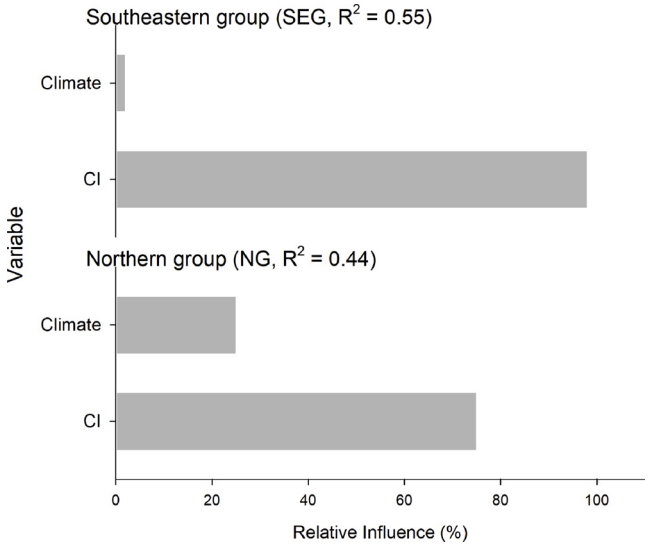

Fig. 6. Relative contributions of climate and competition on tree radial growth of northern group and southeastern group. CI indicates competition indices. For the southeastern group, Climate means 20-year averaged precipitation in September northern group, while for the Climate means 25-year averaged sunshine duration in October,.

growth in the integrated period of 15–25 years. Similar results were found in North America (Filipescu and Comeau, 2007a; Huang et al., 2013) and Europe (Gómez-Aparicio et al., 2011). As a fast growing species, *P. massoniana* forest will be defined as a mature forest when the stand age is near 40 years old (Chen et al., 2004). More than 15–25 years ago, when the subject trees were still young, they were more sensitive to competition. As the subject trees grow up and become more competitive, the climate comes more restrictive. This is probably the reason why 15–25 years cumulated BAI were modeled better. In addition, previous studies found that large subject trees were not sensitive to competition (Canham et al., 2006; Gómez-Aparicio et al., 2011). However, such phenomena were not found in this study region, which indicated that in wet and warm subtropical region, competition may be the most important factor to tree radial growth.

Competition indices considering thicker trees only (NGR, SDBHGR and SBAGR) were the best predictors for fitting radial growth of trees, indicating that the thicker trees were the major source of competition, especially the stem density. Similar results were also found in other studies (Coomes and Allen, 2007; Huang et al., 2013; Lines et al., 2012; Newsome et al., 2006). While in forests with rare human disturbance as in our study forests, tree density and size would be coupled through self-thinning rule (Yoda, 1963), which would make the density and size of thicker competitors perform well in modeling tree radial growth.

Besides, for a given predictor (NGR or SDBHGR), the simulated BAI at different time intervals were very consistent, as indicated by similar conditional R-squares ranging from 0.59–0.69 for SEG and 0.35–0.49 for NG. These results suggested that the subject trees might have a relatively constant pressure of competition as they grow up when their neighbors grow up. This confirmed our hypothesis (cf. Method) and indicated that our results were reliable.

4.3. Spatial patterns of the effects of competition and climate on tree radial growth

For both SEG and NG, the LMM results showed that the conditional R-squares were higher than marginal R-squares, which indicated that the random effects partly explained the variances of subject trees growth (Tables 4 and 5). The random effects in mixed models were estimated by correlation of clustered data (individual trees in each plot here) and mainly reflected the common environmental variances (Huang et al., 2014; Pinheiro and Bates, 2000). The R-squares of full linear models with both competition and climate (0.55 and 0.44 for SEG and NG respectively) were higher than the marginal R-squares (0.45 and 0.26) but lower than the conditional R-squares (0.69 and 0.49), indicating that the climates partly explained the random effects. The higher relative contributions of competition than that of climate for both SEG and NG indicated that competition was the major factor in affecting trees radial growth, which also have been found in other areas (Gómez-Aparicio et al., 2011; Sánchez-Salguero et al., 2015). From southeastern region to northern region, the relative effect of competition decreased while the effect of climate increased. The possible reason was that the climate in southeastern region was wetter and warmer, which is more suitable for tree growth than in northern region. As a result the major pressure came from neighbors for competing resources. While in northern region, trees were more sensitive to climate factors (October sunshine duration) than in southeastern region (September precipitation), which makes the relative importance of climate increase from southeast region to north region. This has been confirmed that different competition levels changed the sensitivity of trees to climate (Linares et al., 2010; Martinbenito et al., 2011; Sánchez-Salguero et al., 2015).

5. Conclusion

Understanding effects of competition and climate on trees growth is critical to assess forest dynamics and succession. Here we combined methods at different levels (individual, site and region levels), for the first time, to explore the effect of tree-tree competition and climate on radial growth of *P. massoniana* in subtropical regions of China. And the relative contributions of competition and climate were further quantified. We found that size and density of trees are more accurate predictors for radial growth of *P. massoniana*. Our combined methodology is a novel method or an attempt to disentangle the contribution of climate and competition to tree growth over the studied region, which is a valuable contribution to the field of forest ecology given limited documentation to detect the effects of climate and competition on tree growth. These findings improve our understanding of the effects of major driving forces on tree radial growth in China subtropical forests, and allow us to make afforestation and deforestation measures more scientifically.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agrformet.2019.04.014.

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